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PERSPECTIVES

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Scientific research at the Laboratoire Arago (Banyuls, France) in the twentieth Century: Edouard Chatton, the "master", and André Lwoff, the "pupil"

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Abstract Edouard Chatton (1883–1947) began his scientific career in the Pasteur Institute, where he made several important discoveries regarding pathogenic protists (trypanosomids, *Plasmodium*, toxoplasms, *Leishmania*). In 1908 he married a "Banyulencque", Marie Herre; from 1920, he focused his research on marine protists. He finished his career as Professor at the Sorbonne (Paris) and director of the Laboratoire Arago in Banyuls-sur-mer, where he died in 1947. André Lwoff (1902–1994) lived several scientific lives in addition to his artistic and family life. But it is the study of protists that filled his first life after he encountered the exceptional Master who was Chatton. Lwoff's father was a psychiatrist and his mother an artist sculptor. He became a Doctor of Medicine in 1927 and then a Doctor of Sciences in 1932, his thesis dealing with biochemical aspects of protozoa nutrition. He met Chatton in 1921 and – until Chatton's death – their meetings, first in Roscoff and then in Banyuls-sur-mer, were numerous and their collaboration very close. Their monograph on apostome ciliates was one of the peaks of this collaboration. In 1938, Lwoff was made director of the Microbial Physiology Department at the Pasteur Institute in Paris, where he began a new life devoted to bacteria, and then to viruses, before pursuing his career as director of the Cancer Research Institute in Villejuif (France). Lwoff was awarded the Nobel Prize in Physiology or Medicine in 1965. He died in Banyuls in 1994. "Master" and "pupil" had in common perseverance in their scientific work, conception and observation, a critical sense and rigor but also a great artistic sensibility that painting and drawing in the exceptional surroundings of Banyuls-sur-mer had fulfilled.

Keywords History of science · Protozoology · Laboratoire Arago · Edouard Chatton · André Lwoff

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I would like to draw the reader's attention to the considerable contribution to Science of these two great researchers, Edouard Chatton – the "master" – and André Lwoff, –the "pupil". I never met Chatton, but he was very familiar to me. My thesis director, protozoologist Pierre-Paul Grassé, gave me as a thesis subject the intracellular study of some phytoplanktonic protists, the dinoflagellates, especially the parasitic blastodinids discovered by Chatton at the beginning of the twentieth century. So I knew Chatton through his publications and his splendid drawings, especially on "class-boards" for his students, class-boards which were bequeathed to the Arago Laboratory in Banyuls-sur-mer and to the Museum of Natural History of Perpignan (Fig. 1). On the other hand, I got to know Lwoff very well; he having been one of my teachers in Banyuls. This paper pays homage to them both.

Edouard Chatton (1883–1947) was born in Romont, Switzerland. When Chatton was very young, his grandfather initiated his interest in biological sciences and was at the origin of his scientific vocation. After high school in the region of Belfort (France), he continued his studies in France at the University of La Sorbonne, in Paris, where the teaching of Professor Yves Delage (1854–1920) fascinated him. Biologist Yves Delage was the discoverer of artificial (chemical) fertilization. He was an assistant to Henri de Lacaze Duthiers, founder of the Roscoff and Arago Laboratories. During a stay in the laboratory at Roscoff in 1902, Chatton was enthralled by the marine fauna and he came back every year to work in the laboratory there. In 1905, working at the Laboratoire Arago in Banyuls, he discovered very strange myxotrophic parasites of the digestive tract of pelagic copepods, the blastodinids. These brilliant results were immediately published, and zoologist Maurice Caullery (1868–1958),

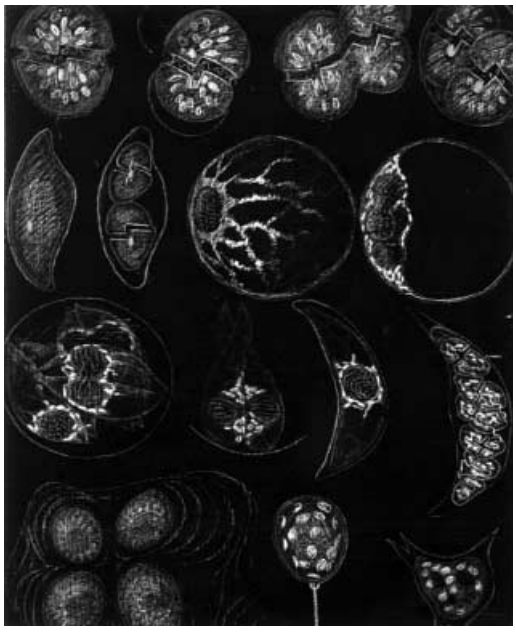

Fig. 1. Free-living dinoflagellates of the genus *Pyrocystis*. Drawing by Chatton for one of the numerous "class-boards" composed for his students (see also the color picture on the cover of this issue)

expert in invertebrates and a Professor at the Sorbonne, Paris, persuaded him to join the department of Protistology and Colonial Microbiology of the Pasteur Institute in Paris, which at that time was directed by Félix Mesnil (1868–1938). Mesnil was a microbiologist, protozoologist and expert in the study of trypanosomes, the agent of sleeping sickness. In 1913, Charles Nicolle (1866–1936), director of the Pasteur Institute in Tunis and a specialist in the study of *Leishmania* (trypanosomids responsible for the severe infectious disease, kala-azar) who was awarded with the Nobel Prize in Physiology or Medicine in 1928, put Chatton in charge of the etiological study of the toxoplasmosis disease (*Toxoplasma gondi*). Chatton was in Tunis when war broke out in 1914. He came back to France, where he was wounded. He then returned to Tunisia where, in Gabes, he founded the Laboratory of Bacteriology of South Tunisia. In 1918, he became the associate and then, for one year, the deputy of Charles Nicolle, in charge of the Pasteur Institute in Tunis. Before the war, Chatton had returned every year to spend his vacation at Banyuls, at the Arago Laboratory, where he prepared his doctoral thesis devoted to parasitic dinoflagellates, which was published in 1920. In 1908, he married Marie Herre, from Banyuls; they had two children, Pierre and Jeanne. Mrs. Chatton-Herre became first his pupil and then his faithful collaborator.

After the war, Chatton was promoted to Master of Conferences at the Louis Pasteur University in Strasbourg. This post was relevant to the chair of General Biology occupied by Eugene Bataillon (1864–1953), famous biologist and discoverer of traumatic parthenogenesis, to whom he succeeded in 1922, before assuming management of the Zoology and Biology Institute of Strasbourg. Ten years later he again succeeded Bataillon as Professor of Zoology and General Biology at the University of Montpellier and as director of the Marine Station of Sète. He was very happy about this: "During my stays in Paris and Strasbourg – said Chatton – I spent all my holidays in Banyuls, Roscoff, Villefranche, Wimereux, but I had found there neither the necessary continuity to lead my works to their outcome nor to undertake some of what I had conceived." In 1937, he assumed the chair of Marine Biology at the Sorbonne in Paris and became the Director of the Arago laboratory in Banyuls. He died in Banyuls on April 23, 1947.

Anyone who has skimmed through the impressive "*Notice of titles and works*", written by Chatton for his accession to the Sorbonne Chair, cannot fail to be dazzled by the multitude of new and various results and by the originality of the concepts. A list of all the discoveries described in the 250 publications would be too long, so I will quote only the main findings. In the Pasteur Institutes of Paris and Tunis, Chatton made many discoveries concerning pathogenic protists. He devoted the rest of his professional life to marine protistology, describing 65 new genera and 145 new species. During his whole career, when not working alone, Chatton worked and published with numerous students and collaborators (Table 1). [A complete list of Chatton's works can be requested from the author, from whom CD ROMS, in both French and English, will be also available separately for the life and publications of E. Chatton and A. Lwoff.]

André Lwoff (1902–1994) was born in Ainay-le Chateau, Allier, France. Lwoff inherited an inclination for hard work and independent thought from his father, who was a physician and a practicing psychiatrist. He joined the Pasteur Institute in Paris as a recipient of a grant for his own research in 1921. Successively assistant (1925) and head of Laboratory (1929), he became a Doctor of Medicine in 1927 and Doctor of Sciences in 1932. His thesis dealt with the study of the nutritional biochemistry of free-living and parasitic protozoa. From 1920 on, he spent his vacations in the Marine Biological Station of Roscoff, where, in 1921, he met Chatton, who became his mentor and friend. Their collaborative work on the study of ciliates and other protists continued every year in either Banyuls-sur-mer, Roscoff, Wimereux or Sète until Chatton's death. The masterpieces of the protistological work of Lwoff include studies of the life cycle, morphology, physiology and morphogenesis of both the apostome (1934) and thigmotrich ciliates (1942–1949). The apostome monograph was almost entirely completed at the Laboratoire Arago (Banyuls-sur-mer). In 1930, Lwoff and Chatton published a silver impregnation technique which has been fundamental to studies of ciliate infraciliature. Since 1929, his wife Marguerite, who died in 1979, had been a close collaborator of Lwoff, with whom she coauthored numerous articles. [A complete list of Lwoff's works can be requested from the author.]

Table 1. Main collaborators of Edouard Chatton

François Picard (1908–1909): Parasitic Laboulbeniaceae
Eugène Allilaire (1908): *Leptomonas* and *Trypanosoma*
Ernest Brement (1909–1915): Copepods parasitic of ascidians
Emile Roubaud (1909–1913): Amoeba of mosquito
B. Collin (1910): Acinetian commensal of copepods
A. and M. Leger (1911–1912): Eu- and Leptotrypanosomids
Krempf (1911): Microsporidia (Octosporea) of muscids
Lalung-Bonnaire (1912): Amoebae, *Vahlkampfia*, newgenus
Pierre Delanoe (1912): Crithidia (*Trypanosoma*, flagellate)
Charles Perard (1913, 1919–1921): Schizophytes of *guinea pig* caecum (Metabacterium). Nicollelidae (parasitic ciliates of Gondi and Daman intestine) Publications with Félix Mesnil (1913): Toxicity of Sarcosporidia extracts (Sporozoa)
Georges Blanc (1914–1919): *Leishmania* bodies in the gecko. A new hematozoa, *Pirhemocyton tarentolae*. Publications with Charles Nicolle (1914–1917): *Leishmania tropica* in culture. Conservation of its virulence for humans
Manceaux (1917): *Toxoplasma gondii*
René Broc (1918): Treatment of amoeba pathology by using bismuth
H. Harant (1922–1925): Parasitic copepods of Ascidians
Marie Chatton-Herre (1923–1929): Natural and experimental factors leading to sexuality in ciliates
André Lwoff (1921–1932): Many papers on ciliates
Robert Courrier (1921–1924): Schizotrypanosomids of bats
P. de Beauchamp (1923–1925): Freshwater Pelagic ciliates
M. Aubertot (1924): *Leptomonas* of the *Drosophila* intestine
Robert Weill (1924): Flagellar apparatus of the plurinucleate peridinian *Polykrikos*
Maurice Parat (1924): Biochemistry of ciliate pigments (*Spirophrya*, *Polyspira*, *Gymnodinioides*)
Louis Tellier (1927, 1929–1934): Limits and resistance of freshwater ciliates to NaCl; action of acids and of arsenic on ciliates
Marguerite Lwoff (1929–1932): Metamorphosis of *Foettingeridae* ciliates, infraciliature of *Podophrya*
Pierre-Paul Grassé (1929): Fine structure of *Polykrikos*
Lucienne Dehorne (1929): Sporozoa of the genus *Siedleckia*
Raymond Poisson (1931): *Hematodinium perezi*, parasitic peridinian of crab blood
Louis Rapkine (1931): Appearance of SH groups before division in *Foettingeria* ciliates
Jacques Monod (1931): Mouth beginning in dividing ciliates. Genetic continuity of the ciliary system in the ciliate *Chilodon*
Simone Brachon (1933, 1935, 1936): *Paramecium duboscqui* with two races. Argentophilic structure and infraciliate in ciliates. Mitochondria of cilia and parabasal apparatus. Cinetome of *Opalina*
Raymond Hovasse (1934): Ectoplasmic net in *Polykrikos*
Berthe Biecheler (1934–1936): Parasitic peridinians. Chromatic cyclosis of peridinians
Joséphine Seguela (1936): Hypotrich ciliates of the branchia of *Ciona*
Felix and Simone Villeneuve (1936–1937): Sexuality and evolutive cycles of Sporozoa. Morphogenesis of the mouth of peristome ciliates
Odette Tuzet (1941–1943): Spermiogenesis of *Lumbricidae*

In 1938, Lwoff was appointed director of the newly created Department of Microbial Physiology at the Pasteur Institute, where he remained until 1968. There, he studied nutrition and growth factors in bacteria. This led him to investigate bacteriophages, prophages and other viral particles. His dedication to clarifying the biological and genetic nature of bacteria and viruses led him away from the field of protistology to which he never returned, except at the end of his life. Lwoff became an undisputed master in the young science of virology, and contributed to the development of the viral concept. Furthermore, his observations and hypotheses on lysogeny, and especially on the factors influencing the development of viral diseases (the carcinogenic agents which induce pro-virus to virus transformation) strongly influenced medical research in the study of cancer.

From 1959 to 1968, Lowff held the Chair of Microbiology at the Faculty of Sciences in Paris and then became the Director of the Scientific Research Institute (CNRS) in Villejuif (1968–1972). His retirement in 1972 allowed him to devote more time to his beloved old hobby, oil painting. Doubtless the hilly yet wide landscape, especially near Banyuls-sur-mer, together with the Mediterranean light and the colors of the scrubland flowers and trees inspired his beautiful paintings. Living several months a year in his austere and majestic fortress (the *Mas Guillaume*) which overlooked the Bay of Banyuls, he often visited our laboratory and was always interested in our latest results on the cell biology of dinoflagellates and other protists. Giving freely of his advice, he always impressed us with his rigorous reasoning.

During the summer of 1921, Chatton was Master of Conferences at the Zoological Station of Roscoff. The following year, he became Professor at the University of Strasbourg, where he had taught General Biology in the Faculty of Sciences. He looked for a young collaborator to assist him in his protistological research. He also had the task of recruiting an assistant for the Pasteur Institute in Paris. André was 19 years old and Chatton 38. Their collaboration was immediate and successful and indeed at the end of the year a first note, concerning a new family of Ciliate Acinetians, was published at the Science Academy in Paris. The relationship of master to pupil was above all very friendly and extremely fruitful. Of the 151 publications of Lwoff with regard to protistology, 55 were brought about by collaboration with Chatton, in particular the *Monography of apostome ciliates*, published in 1935 (450 original pages) and that of thigmotrich ciliates, published in 1949 and 1950, after the death of Chatton (Table 2).

Table 2. Main works of André Lwoff on protistology

Numerous descriptions of families, genus and species of ciliates, mainly from sea water, parasitic or phoretic (Thigmotrichidae, Peritrichidae, Apostomidae, Acinetians, Trichostomatidae)[a]
Study of their evolutive cycle[a]
Study of the nutrition in ciliates (1923)
First pure culture of a Ciliate (1923)
Infraciliatures and genetic continuity of the recessive ciliary systems : the concept of its genetic continuity is expressed for the first time (1923)[a]
Silver impregnation technique (1930): fixation, inclusion in agar, Ag nitrate + light[a]
Biochemical research on protozoa nutrition (1932, thesis): Concepts of physiological evolution and of loss of functions are expressed for the first time in the light of the results obtained on free living and parasitic ciliate nutrition
Apostomes ciliates (1934): Parasitic ciliates with two hosts and showing remarkable ciliary metamorphoses[a]
Law of the Desmodexy. Hypothesis of the genetic continuity of kinetosomes. Morphogenesis of Trichocysts[a]
The physiological evolution and the loss function in microorganisms (1944)
Thigmotriches ciliates (1942, 1949), commensal or parasitic of molluscs. Morphology and morphogenesis[a]
Problems of morphogenesis in ciliates (1947–1950)
The physiological evolution and the loss of function in microorganisms (1944)
Problems of morphogenesis in ciliates (1947–1950)

[a]With E. Chatton

Their love of marine biology and for marine protists led Chatton and Lwoff to spend their vacations in the marine stations at Roscoff or at Banyuls, passing through Villefranche, Sète and Wimereux. Chatton, with his scientific rigor, was for Lwoff an incomparable initiator. They met in Roscoff every summer until 1929 and Marguerite Lwoff was then associated with their research. Chatton wrote that his first stay in Roscoff in 1902 was for him ''the revelation of a new world'' that determined the scientific orientation of his life.

Between 1920 and 1930, Chatton attracted leaders in the field such as Paul Wintrebert, Emmanuel Fauré-Fremiet, Jean Cantacuzène, Constantin Davydoff, Paul Marais de Beauchamp and Charles Perez to Roscoff and Banyuls; the companions of Lwoff at Roscoff Station were Robert Courrier, Boris Ephrussi, Maurice Fontaine, Jean Piveteau, Marcel Roubault, Georges Teissier, Etienne Wolff and René Wurmser, who all went on to become distinguished teachers in the field.

At that time, Roscoff Station was a typical small Breton port, with granite houses and a church. It was chosen as the seat of a great marine laboratory because of the amplitude of tides and the variety and biological wealth of the coastal facies in which abundant rocks, sands, herbarium and sludge bench coexist. ''In this paradise of marine zoology'', according to Lwoff's friend, the physician and naturalist Jacques Millot, ''all the favorable conditions to a free and sound work were combined''.

Jacques Millot described Lwoff very well: ''Physically, he was out of the ordinary: tall, blond, a halo of abundant golden hair a bit curly, so that when he tilted his head with his characteristic half-smile, he called to mind the famous angel of the Reims Cathedral. This angelic aspect, nuanced with an apparent nonchalance was not exempt of a romantic look. Early intellectual talents emerged by his exceptional ability to observe and interpret the smallest structural details of protozoa as revealed by the microscopes of the time and the reconstruction of evolutive cycles of unicellular preceding the understanding of the more complex mechanisms of the protozoan cell biology. The deceptive nonchalance of his behavior, hid a critical eye and spirit always alert, accompanied by a great facility and relentlessness for his work'' (Fig. 2).

Fig. 2. André Lwoff's mischievous and angelic smile. (From: Monod J, Borek E (eds) (1971) *Of microbes and life*, Columbia University Press, New York)

However, it was in Banyuls that their destiny was sealed. Jacques Millot wrote for the Scientific Jubilee of André in 1971: "Whatever the fruitful activity of the team Chatton-Lwoff in Roscoff and the importance of their discoveries in this place, work is carried on brilliantly and notably extended in the Laboratoire Arago of Banyuls, Catalan rival of the Breton Institute of Roscoff. Of comparable importance, devoted to the same tasks, both establishments mutually collaborated while in opposition in many respects, each of them having its own personality. Almost everything contrasted between them: not only the hot and dry, sometimes burning climate of the Roussillon, very different from the mild and moist Brittany, which modified the work calendar. In Banyuls, the very hilly hinterland, covered with vines, orange trees, olive trees, pines, helms, cork-oaks, the bright light, the scrubland scents distilling their essences under the sun, the picturesque vineyards as in Spain, the opposition between the Mediterranean curved tiles and the Breton slates, between the Catalan personality compared to that of the Finistère, even the morphology of Catalan women immortalized in stone and bronze by Aristide Maillol, great sculptor born there, everything contributed to make the atmosphere of Laboratoire Arago much more attractive environment than that of Roscoff, which could appear sadder for some."

As to the Mediterranean fauna, Chatton and Lwoff identified numerous unicellular organisms of sea-water, described them, and analyzed their evolutive cycles, accumulating many discoveries. Most of their research on apostome ciliates was carried out in Banyuls. There are parasitic ciliates with two hosts, evolving in crustaceans and in coelenterates (sea anemones) and with a remarkable ciliary metamorphosis. On this selected material, they proposed the "Desmodexy" law: on all ciliates, the kinetodesm is always located at the right of the kinetosome rows. They also proposed the hypothesis of the genetic continuity of the kinetosomes. The kinetodesm is the fribrillar wrapping linking together kinetosomes, which are themselves organized into a ciliary chain or kinetie.

In 1923, the director of the Laboratoire Arago was the protistologist Octave Dubosq, the predecessor of Chatton. Dubosq was a teacher of Pierre Paul Grassé. Grassé became a famous protozoologist, author of the impressive "*Traité de Zoologie*". Lwoff had got to know Grassé in Banyuls, the former working with Dubosq, the latter with Chatton; some kind of rivalry arose between the two protistologists. Lwoff's first publications date back to 1925, when he became assistant researcher at the Pasteur Institute in Paris. He published the beginning of his science thesis on the utilization of glucids by some protozoa and on the feeding of ciliates on dissolved substances. In 1927, he defended his medical thesis before becoming director of the Laboratory in 1929. During this time, the studious vacations in Roscoff and in Banyuls followed one another and publications with Chatton continued. From 1929, Marguerite Lwoff, his wife and close collaborator, began to work with them. Note that from very morphological descriptions of new families or genera of ciliates, Chatton and Lwoff moved more and more toward problems and concepts of cell biology. In 1931, they searched for the genetic continuity of the ciliate systems of Foettingeridae ciliates. More recently, in 1976, Dippel, to demonstrate this hypothesis, suggested the presence of DNA or RNA or of an intrakinetosomal chromosome. This hypothesis is now obsolete, a new path of research having been opened with the hypothesis of transmission by means of a proteinic template. Indeed, the reproduction of kinetosomes imposes not only the reconstitution of a microtubular edifice with a particular and stable geometry but also the conservation of the original polarity. This terminology of template was formerly used by Lwoff in 1950 in his book "*Problems in morphogenesis in ciliates*". Groups of researchers such as those led by Anne Fleury and Michel Bornens currently study cellular and molecular aspects of the morphogenesis of basal bodies or kinetosomes. Confocal laser microscopy or transmission electron microscopy, biochemistry and molecular biology have confirmed and completed Chatton and Lwoff's observations on ciliate morphogenesis. Moreover, a new aspect of the morphogenetic role of kinetosomes was evidenced by Ruiz et al., after the inactivation of the centrin genes *ICL1a* and *ICL1b* [Ruiz F, Vayssie L, Klotz C, Sperling L, Madeddu L (1998) Homology-dependent gene silencing in Paramecium. Mol Biol Cell 9:931–94]. In inactivated cells, the infraciliary net is disassembled, which reveals the presence of a precise interaction zone located between kinetosome and infraciliary net elements. When the *ICL1a* and *ICL1b* genes are reactivated, the net is reconstituted from these residual elements (Fig. 3).

Chatton and Lwoff researched other problems of morphogenesis such as the formation of the posterior oral aperture in dividing ciliates and its relationship in continuity with the anterior mouth. In 1931, they also described the appearance of SH-groups just before division in Foettingeridae ciliates. In 1930, they published a very useful technique for the study of infraciliature: silver impregnation after cytological fixation and without desiccation. The material is either fixed with osmium or not, then embedded in agar, submitted to $AgNO_3$ then exposed to the light of a mercury lamp. This technique is still used today. In ciliates, an immense experimental work was accomplished together with Marie Chatton: they discovered that the determinism of the evolutive cycle progress could be conditioned by the external medium. They showed that, in *Paramecium*, the sexual cycle could be started by external factors such as inanition, calcium, lactic acid and pH, acting jointly. This theory opposes the American theory of Mopas-Sonneborn which attributes sexuality exclusively to genetic factors. However, one theory does not exclude the other...

In 1932, Lwoff defended a brilliant thesis of science entitled "Biochemical research on the nutrition of

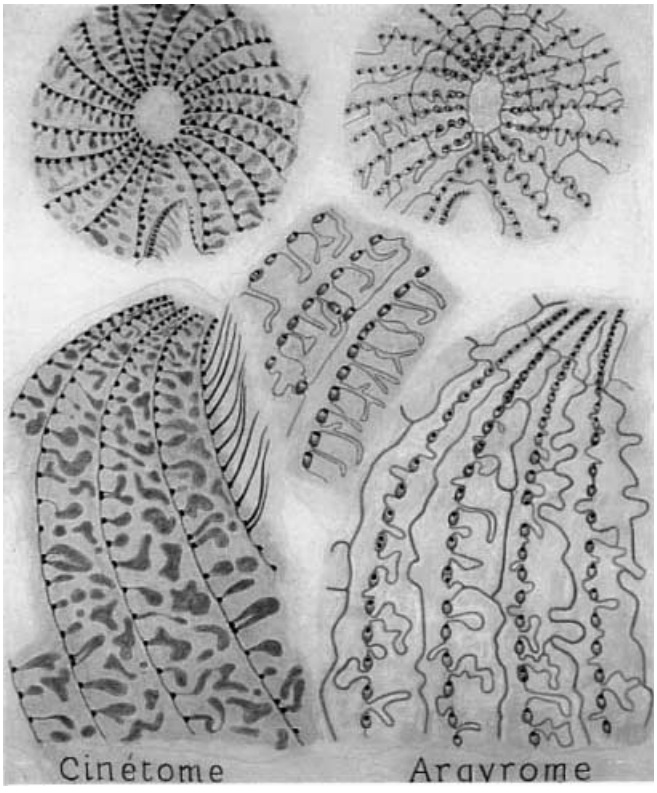

Fig. 3. Organization of the ciliate's infraciliary net from Chatton and Lwoff's work. Chatton's drawing on class-board

Protozoa''. By then he had already published 76 papers in protistology. The role of Lwoff working with Chatton went beyond that of a brilliant ''second'' and he quickly moved from ''pupil'' to associate (Fig. 4). He became one of the essential driving forces in this field before turning toward the new horizons of microbial physiology in 1938 when he became the Chair of the Department of Microbial Physiology, created especially for him at the Pasteur Institute in Paris. Nevertheless, he never forgot his dear protists. Indeed, he published a memorandum on thigmotrich ciliates in 1949, and again in 1950, and from 1947 to 1950, he taught regularly in the United States at Harvard Medical School on ''Problems of morphogenesis in ciliates''.

Lwoff, an exceptional scientist, was also a talented artist. He exhibited his paintings in an art gallery in Paris: his last exhibitions being held in 1978 and 1985. A good-hearted man, he had a great, sometimes biting, sense of humor, but he was always kind and helpful to

Fig. 4. The ''Master'', Edouard Chatton, and his collaborator, André Lwoff, in Banyuls-sur-mer, 1938. (Photograph, Archives of the Arago Laboratory)

those whom he befriended. When, in 1965, he was awarded the Nobel Prize in Physiology or Medicine, which he shared with François Jacob and Jacques Monod, many scientists were unaware that Lwoff had first been a great protozoologist before becoming a great microbiologist and then virologist. I learnt about his artistic talents in Banyuls, where I met him and his wife, Marguerite, in 1971 when he was still the Director of CNRS, Villejuif, and when he had just acquired the *Mas Guillaume*. In 1971, I had just defended my doctoral thesis on the cell biology of free-living and parasitic dinoflagellate protists, especially blastodinids, which were discovered and described by Chatton. With the help of an electron microscope, I had been able to verify and validate many hypotheses proposed by Chatton, including the syndinian mitosis and the permanence of the nuclear envelope during dinomitosis. When Lowff read my thesis, he asked me to rewrite and organize an unfinished manuscript by Chatton. Chatton's work on *Paradinium*, a parasite phylogenetically close to Mycetozoa, was completed by my own observations and this led to an article co-authored by Chatton and myself, which was published in 1973 with a preface by Lwoff.

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